Acta Geologica Polonica, Vol. 60 (2010), No. 2, pp. 219–229

The myth of the Triassic lytoceratid ammonite *Trachyphyllites* Arthaber, 1927, in reality an Early Jurassic *Analytoceras hermanni* Gümbel, 1861

RENÉ HOFFMANN[1] AND HELMUT KEUPP[2]

Freie Universität Berlin, Department of Earth Sciences, Institute of Geological Sciences, Branch Palaeontology, Malteserstrasse 74-100, Building D, 12249 Berlin, Germany.
E-mails: [1] *mind@zedat.fu-berlin.de;* [2] *keupp@zedat.fu-berlin.de*

ABSTRACT:

Hoffmann, R. and Keupp, H. 2010. The myth of the Triassic lytoceratid ammonite *Trachyphyllites* Arthaber, 1927, in reality an Early Jurassic *Analytoceras hermanni* Gümbel, 1861. *Acta Geologica Polonica*, **60** (2), 219–229. Warszawa.

The ammonoid "*Trachyphyllites costatum"* Arthaber (1927), based on a single specimen from an erratic boulder of presumed Late Triassic (Norian age) from Timor, (Indonesia), was originally described as a phylloceratid but later recognized as a true lytoceratid by Basse (1952) and Schindewolf (1961), and used by Wiedmann (1966a, 1966b, 1970) to support his idea of a polyphyletic origin of the post-Triassic ammonoids and of the Late Triassic roots of the lytoceratids. New collections of additional specimens and associated taxa from other erratic boulders in the type locality have confirmed observations (Tozer 1971; Krystyn 1978) that the age of the original boulder was misinterpreted, and have shown that "*Trachyphyllites"* is actually of Early Jurassic (Hettangian) age.

An unpublished generic revision of the entire superfamily Lytoceratoidea by Hoffmann (2009) has shown that "*Trachyphyllites costatum* Arthaber" is a junior synonym of *Analytoceras hermanni* (Gümbel, 1861), a taxon thought by Wähner (1894) to be a subjective synonym of *Analytoceras articulatum* (J. Sowerby, 1831) We reestablish the species *Analytoceras hermanni* (Gümbel, 1861) for *Analytoceras articulatum* "Type B" (Wähner 1894), which is characterized by a wide umbilicus and a small whorl expansion rate. The morphologically distinct "Type A" (Wähner 1894) corresponds to the type species of *Analytoceras, A. articulatum* (J. Sowerby, 1831). A revised phylogeny of the Early Jurassic lytoceratids is presented.

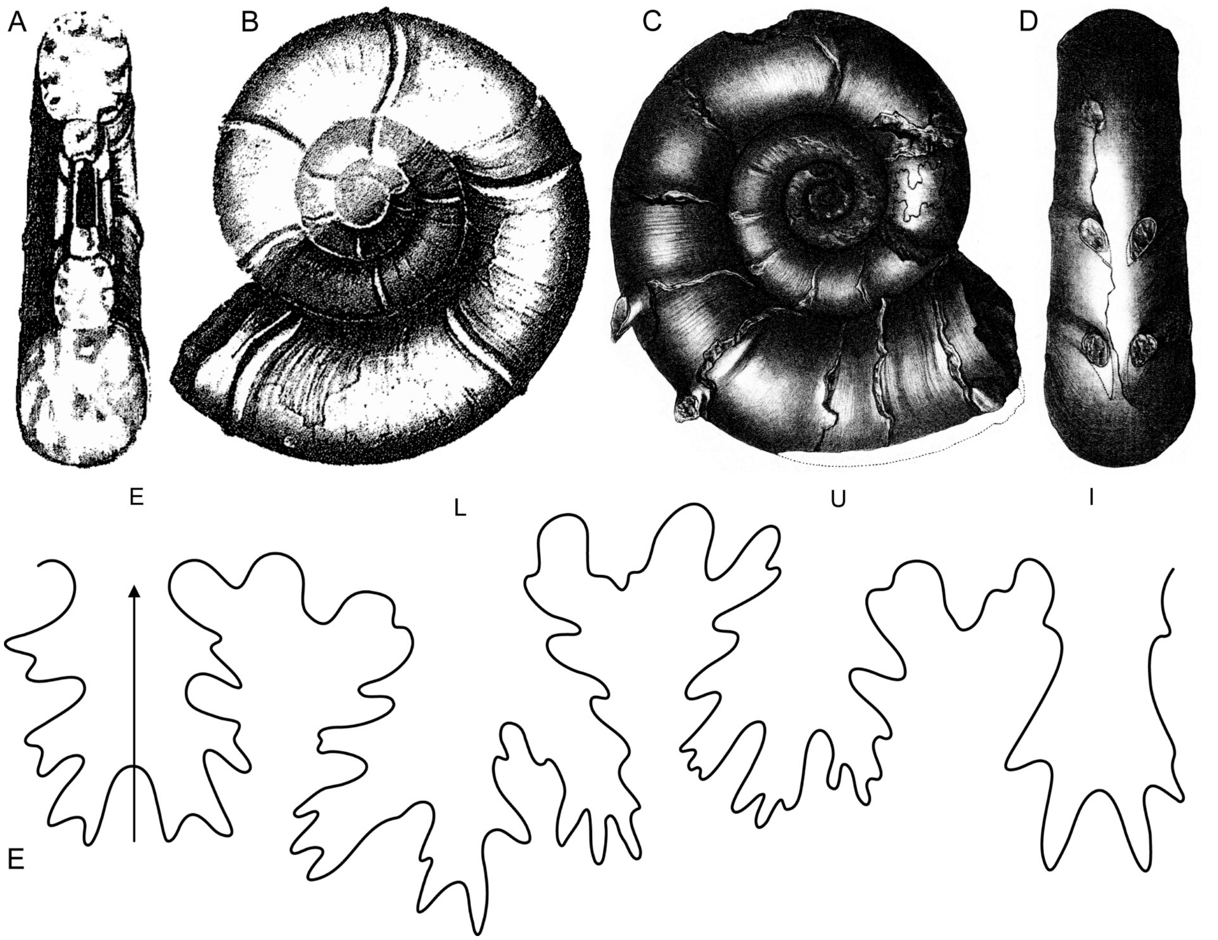
Key words: Jurassic; Lytoceratoidea; *Trachyphyllites*; Phylogeny; Systematic; Timor.

INTRODUCTION – HISTORY OF AN ERROR

Arthaber (1927) introduced the new taxon "*Trachyphyllites costatus*" (Text-fig. 1A, B) based on a single ammonoid fragment from an erratic boulder of the Bihati river near Baun/SW Timor, which was collected by the Dutch expedition to Indonesia (Dutch East-Indies) during 1916 and thought by him to be of Late Triassic (Norian) age. He classified his new taxon originally within the Monophyllitidae as a subgenus of *Monophyllites* and interpreted the similarities with Early Jurassic lytoceratids as possible analogies. Spath (1934) classified the monospecific genus "*Trachyphyllites*" within the more progressive phylloceratid family Discophyllitidae owing to the complex suture line showing subdivided saddles (Text-fig. 1E). This systematic position was accepted by Arkell *et al*. (1957), Orlov (1958) and Houša (1965). Basse (1952) and Schindewolf (1961, p. 722) first postulated the systematic position of "*Trachyphyllites*" in the Lytoceratoidea on the basis of analysis of the suture line and thought that, in consequence of the presumed Norian age of the single specimen of "*Trachyphyllites costatus*", the development of lytoceratids started from phylloceratid ancestors early in the Triassic. The subsequent classification of "*Trachyphyllites*" within the lytoceratids can be traced back to Wiedmann (1964, 1966a). He established the monospecific family Trachyphyllitidae (nom corr. ex Trachyphylloceratidae Wiedmann 1966a, Shevyrev 1968) as the proposed stem group of all "Lytocerataceae", this being confirmed by finding weakly fimbriate lineation on the shell of Arthaber's single specimen. This viewpoint was followed by the majority of cephalopod workers, e.g. Schindewolf 1968; Shevyrev 1968; Hölder 1975; Lehmann 1976; Drushchits *et al.* 1976; Kennedy 1977; Kennedy and Klinger 1978; Wiedenmayer 1978, and later by Wiedmann 1981; Besnossov and Mikhailova 1985 and Lehmann 1990.

In consequence of the presumed Norian age of the earliest lytoceratid ("*Trachyphyllites*"), Wiedmann (1966a, 1966b) used this single specimen to support his idea of a polyphyletic origin of the post-Triassic ammonoids and of the Late Triassic roots of the lytoceratids (Wiedmann 1966a, 1966b, 1970). According to this concept, the lytoceratid lineage would have arisen from the Skythian *Leiophyllites/Eophyllites* stock (Teichert 1967; Wiedmann 1970). In any case, this evolutionary concept for post-triassic ammonoids had been already rejected by Tozer (1971a, 1971b).

After the position of "*Trachyphyllites*" among the lytoceratids had been generally accepted by Houša (1965), Teichert (1967), Schindewolf (1968), Shevyrev (1968) and Kennedy (1977), Tozer (1971a, 1971b) first expressed doubts concerning the correct stratigraphic assignment of the erratic boulder from Timor in which the



Text-fig. 1. Comparison of "*Trachyphyllites costatus* Arthaber" and "*Ammonites*" *Hermanni* Gümbel. A-B – Original illustrations of the artificially completed specimen of "*Trachyphyllites costatus*". A sectional view. B. lateral view; reproduced from Arthaber (1927, pl. 17, fig. 3 a–c). C-D – Original illustrations of "*Ammonites*" *Hermanni* Gümbel, 1861. C – Lateral view, note the simplified suture line. D – ventral view; reproduced from Wähner (1894, pl. 3, fig. 3a–b). E – suture line of "*Trachyphyllites costatus* Arthaber" as presented by Arthaber (1927) and reproduced from Schindewolf (1961, text-fig. 42); from the accepted systematic position of "*Trachyphyllites*" it becomes clear that U is U2 and U1 is between U2 and I specimen of "*Trachyphyllites*" was found. The problems of the condensed beds of the Hallstatt facies were discussed in detail by Wendt (1970) and Tozer (1971b). Welter (1914) was the first who discussed the problems of the Hallstatt facies in Timor. He concluded that the whole of the Upper Triassic was represented by a mere two metres of rock representing a time span of about eight ammonoid-zones (about 10 m. y.). In the Bihati river region, numerous erratic boulders of differing sizes and stratigraphic positions (Permian to Early Jurassic) are incorporated in a Tertiary mass flow deposit. Because the boulders of Late Triassic (Carnian/Norian) and Early Jurassic (Hettangian) age both show a similar Hallstatt facies of grey to reddish limestones containing mainly cephalopod shells covered by black manganese crusts (Keupp 2009), it is very difficult to make correct stratigraphic assignments for individual erratic boulders. It is therefore not surprising that Arthaber, who had never visited Timor and had never seen the boulder from which the *Trachyphyllites* specimen had been removed, assumed incorrectly that it was of Triassic rather than Early Jurassic age. Krystyn (1978) confirmed that "*Trachyphyllites costatus*" was associated with a characteristic fauna of Early Jurassic (Hettangian) ammonites, on the basis of new specimens collected from the type locality during the early 1970s. In consequence of the proof of an Early Jurassic age of "*Trachyphyllites*", the arguments for a polyphyletic origin of the post-Triassic ammonites (Wiedmann 1966b, 1970) and of the Late Triassic roots of the lytoceratids no longer apply and were rejected (Tozer 1981). The recent record of a probable *Trachyphyllites* sp. in the Upper Triassic *marshi* Zone (Lucas and Tanner 2004) is based on the stratigraphic section of the Alps described in Mostler *et al*. (1978) and was again influenced by Wiedmann (1972). However, in view of the highly corroded and badly preserved single specimen of this ammonite, its systematic position is doubtful. Another specimen was recorded by Basse (1968) from Carnian deposits of central Serbia but was not figured and the record is thought to be based on a misinterpretation.

In contrast, the ammonites from the more or less continuous sedimentary sequences across the Triassic/Jurassic boundary of Nevada/USA clearly show the derivation of the lytoceratids from the ammonite family Psiloceratida during the earliest Hettangian and confirm the monophyly of both the Ammonitina Hyatt, 1889 and its component superfamily Lytoceratoidea Neumayr, 1875 (Guex and Taylor 1976; Guex 1987, 1995; Guex *et al*. 2004; Hillebrandt 2000; Shigeta 2006; Hoffmann and Keupp 2008). Despite the fact that "*Trachyphyllites*" is now an Early Jurassic member of lytoceratids, its systematic relationship within the Lytoceratoidea remains questionable. Houša (1965, p. 35) stressed for the first time the necessity of a systematic revision to clarify the position of the genus *Analytoceras* and related forms within the Lytoceratoidea in respect of the presumed derivation from "*Trachyphyllites*". Krystyn (1982) grouped "*T. costatus*" within the Jurassic genus *Audaxlytoceras* Fucini, 1923, and later (Krystyn 1999) treated *Trachyphyllites* as a valid genus, which he placed together with *Analytoceras* in the family Pleuroacanthitidae. This classification was followed by Sprey (2002), while Venturi and Bilotta (2008) still accepted the genus "*Trachyphyllites* Arthaber" classified within the Analytoceratidae Spath, 1927.

NEW MATERIAL FROM BIHATI/ SW TIMOR

During fieldtrips by R. Veit (Velden/Vils) and Dr. W. Weitschat (Hamburg) in 2003 and 2005, and in July/August 2008 by one of the authors (H.K.) together with Dr. W. Weitschat and R. Veit, to the Bihati river region south of Baun, in Amarassi Province, SW Timor/ Indonesia, based on a cooperation contract between the Freie Universität Berlin and the Universitas Gadhja Mada in Yokjakarta, some additional Early Jurassic fossils were collected from smaller erratic boulders (some dm in diameter) on the slope of the Bihati Canyon, including three specimens of "*Trachyphyllites costatum* Arthaber" (Text-fig. 2A–D). These lytoceratids, which are the subject of the taxonomic revision presented herein, were accompanied by a characteristic Hettangian cephalopod association containing, besides other taxa (see Krystyn 1978): *Atractites alpinus* Gümbel, *Paradasyceras uermoesense* (Herbich), *Geyeroceras cylindricum* (Sowerby), *Ectocentrites* cf. *petersi* (Hauer), *Paracaloceras* sp. Smaller boulders also containing *Pseudotropites ultratriassicus* (Canavari) demonstrate that the characteristic Early Jurassic Hallstatt facies ranges up into the Sinemurian. The finds of *Analytoceras articulatum* (Sowerby) as figured by Sprey (2002, pl. 7, fig. 3) from the Krystyn collection, accompanied by *Ectocentrites petersi*, seem to be also of Late Hettangian age, but could not have been found in the same erratic boulders together with "*Trachyphyllites costatum*".

The three new specimens of "*Trachyphyllites costatum*" (Text-fig. 2A–D) are stored at the Freie Universität Berlin, Institute of Geological Sciences, collection Keupp under the numbers: MAn-3218. MAn-1897, MAn-x (= cast of the unnumbered specimen in the R.Veit collection) and labelled *Analytoceras hermanni* (Gümbel, 1861).

Text-fig. 2. Three specimens of *Analytoceras hermanni* (Gümbel) from the Bihati river valley south of Baun, SW Timor (Amarassi Province): A – MAn-x (coll. R. Veit), Ø 101 mm. B – MAn-3218, Ø 81 mm. C – MAn-1897 (leg. R.Veit), Ø 84 mm, on the left side the shell was removed to show the suture line. D – right side of the same specimen

DESCRIPTION OF THE NEW SPECIMENS

The three specimens range in size from 81 to 101 mm and are preserved without the body chamber. The shells have been calcified during diagenesis and appear black owing to a thin manganese crust cover. Also corresponding to the slow sedimentation rate of the “Hallstatt facies”, small crinoid roots were growing *post mortem* on one side of the shells. In all three specimens the centre of the umbilicus, including the ammonitella, has been lost. The umbilicus is wide, about 45 %. Beginning at a shell diameter of about 6 mm, six to seven parabolic ribs per whorl appear. The smooth interspaces between the parabolic ribs show fine retroradiate striae that are finely crenulated (Text-fig. 3).

Text-fig. 3. Finely crenulated striae of *Analytoceras hermanni* (MAn-3218), image section about one cm

After about 80 mm shell diameter, the parabolic ribs (MAn-x) develop more and more flair-like prominent collars and the ventro-laterally parabolic nodes change to long spines with irregular growth-direction like in the holotype of *Analytoceras hermanni* (Gümbel) figured by Wähner (1894, pl. 7, figs 4a–d) (Text-fig. 1C–D). The whorl section is circular to slightly compressed.

The suture line was uncovered by polishing (specimen MAn-1897, Text-fig. 2C and Text-fig. 4) the right flank of the outer whorl between 75 and 84 mm shell diameter (= 30 mm whorl height). It shows a short external lobe (E) and a dominant asymmetrical trifid lateral lobe extending significantly further back than E. The terminal ends of its ventral branch nearly reach the siphonal area. The also deeply incised trifid umbilical lobe (U_2) appears more asymmetrical than figured by Wiedmann (1970), where the suture line of the more juvenile stage of "*Trachyphyllites*" (at 10 mm wh) was reproduced.

DISCUSSION

We agree with Venturi and Bilotta (2008) that all the morphological features of "*Trachyphyllites costatum*" fit the diagnostic characters of the genus *Analytoceras.* This genus was originally established by Hyatt (1900) without any figure, but with *Analytoceras* (*Lytoceras*) *articulatum* Wähner designated as type species. Arkell *et al.* (1957) regarded *Ammonites articulatus* J. Sowerby (in De la Beche, 1831, p. 334, fig. 70) as type species, but reproduced the figure of *Lytoceras articulatum* given by Wähner (1894, pl. 7, fig. 4a–d). Therefore,

Text-fig. 4. Suture line of *Analytoceras hermanni* (Gümbel, 1861) from the Hettangian of Bihati River, Timor at whorl height of 30 mm (MAn-1897, Text-fig. 2C); compare with simplified suture (due to heavy abrasion) of *A. hermanni* (Text-fig. 1C), as presented in Wähner (1894 pl. 3, fig. 3a)

Specimen	D (mm)	wh (mm)	wb (mm)	wh/wb	Uw (mm)	Uw/D (%)	WER
A. hermanni (holotype) after Wähner (1894; pl. 7, fig. 4a-d).	108	33	38	0.87	50	46.3	2.07
"*Trachyphyllites costatus*" (holotype) after	44	14	12	1.17	21	47.7	2.15
Arthaber (1927; pl. 17, fig. 3)	22	7	6.3	1.1	9.6	43.6	2.15
Bihati: MAn-3218	81	26	24	1.08	37	45.7	2.17
Bihati: MAn-1897	84	28	25	1.12	37.7	44.9	2.25
Bihati: MAn-x (coll. R.Veit)	101 (82.5)	33.6 (28.1)	(26.3)	1.07	45.3	44.8	2.30

Table 1. Measurements of *Analytoceras hermanni* (Gümbel 1861) from the Hettangian of Bihati River, Timor in comparison with the holotype from the Northern Alps

based on the original designation of Hyatt (1900), Hoffmann (2009) suggested that the specimen figured by Wähner (1894, pl. 7, fig. 4a–d) and also by Arkell *et al.* (1957, p. L192, fig. 222/2a–d) be chosen as the lectotype of the type species, *Analytoceras articulatum* (J. Sowerby, 1831). The characterization of the genus *Analytoceras* given by Hoffmann (2009) includes the following features:

• Moderate shell size, fairly evolute whorls with an expansion rate of 2.0–3.3 and umbilical width between 32 and 48 % (Text-fig. 5).

• Whorl section circular to slightly compressed.

• Juvenile stages with deep regular, radial to slightly prorsiradiate constrictions associated with fine radial ribs in front of the constrictions also crossing the venter.

• At middle growth stage parabolic ribs curving backwards and crossing the growth lines occur with a great variability. Later stages developing high flare-like parabolic ribs, with associated ventrolateral spines (Text-fig. 2A–D).

• Except for parabolic sculptures, the ornamentation is characterized by very delicate fine striae with weak fimbriation (Text-fig. 3).

• The adult suture line is characterized by a short external lobe (E), reaching about one third of the length of the lateral lobe (L), L and U_2 are trifid and broad (Text-fig. 4). Main saddles (E/L and L/U) are partly asymmetric bifid, all saddles with phylloid endings. The external branch of L ends immediately below the E lobe near the siphuncle area or barely in contact with the broad siphonal band, which is divided by a simple triangular siphonal saddle (Wähner 1894). The internal suture line shows a broad, non-cruciform, bifid internal lobe (I) incised with weak lateral branches. The terminal branches of I are not incised. The internal lobe generates an intermediate septal lobe (Canavari 1888, pl. 9, fig. 8; Salfeld 1924, pl. 3, fig. 1–2).

Analytoceras is stratigraphically restricted to the Hettangian of the Mediterranean–Tethyan area: Austria, central Apennine (Italy), Timor (Krumbeck 1923; Arthaber 1927; Canavari 1882; Wähner 1894; Krystyn 1982; Dommergues 1994; Bertinelli *et al*. 2004).

Morphological affinities, such as the first appearance of weakly crenulated striae (mentioned in "*Trachyphyllites costatus*" for the first time by Wiedmann (1970)) which represent an apomorphic character for *Analytoceras* Hoffmann (2009), and the first appearance of an intermediate septal lobe (Salfeld 1924; Hoffmann 2009) give hints that *Analytoceras* might be the direct ancestor of *Lytoceras* Suess, 1865 (Text-fig. 6).

Wähner (1894) recognized two different morphotypes in *Analytoceras articulatum*, Type A and Type B. Type A corresponds to the lectotype and differs from Type B in less evolute coiling and a significant higher whorl expansion rate. The Type B was first described by Gümbel (1861) as *Ammonites hermanni* (Text-fig. 1C–D) on the basis of an unfigured specimen from the Northern Alps. The same specimen was figured for the first time 33 years later by Wähner (1894, pl. 3, fig. 3a.b, see Text-fig. 1). Besides the morphological differences, Wähner considered both morphotypes to be subjective synonyms. The ornamentation and measurements, particularly the width of the umbilicus and the whorl expansion rate, of all the Bihati-specimens are close to those of Gümbel´s specimen of *Analytoceras hermanni*.

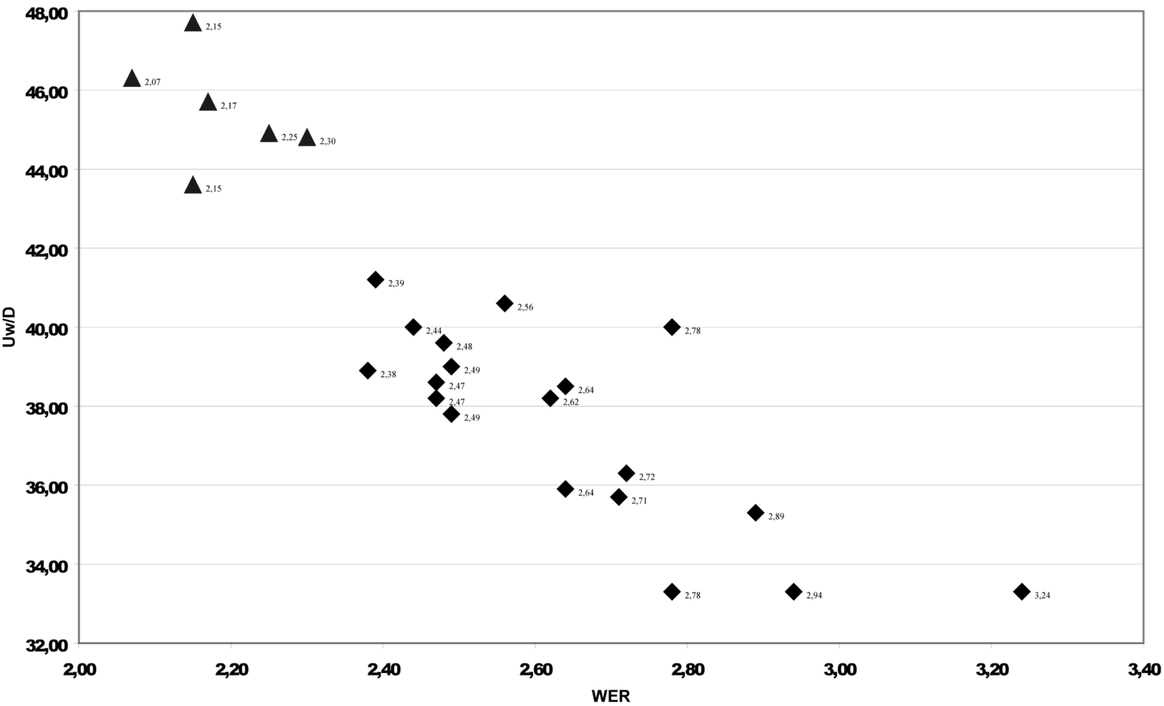
Only the whorl section, which also shows a wide range of variability in *Analytoceras articulatum* Type A (cf. Wähner 1894, p. 45: wh/wb = 0.8–1.25%) differs. Thus, the whorl section is more or less circular, rather slightly depressed in Gümbel's specimen (wh/wb = 0.87), while slightly compressed in the Bihati specimens (wh/wb: 1.07–1.17).

SYSTEMATIC PALAEONTOLOGY

Order Phylloceratida Arkell, 1950 (incl. Phylloceratina and Ammonitina)
Suborder Ammonitina Hyatt, 1900
Superfamily Lytoceratoidea Neumayr, 1875
Family Lytoceratidae Neumayr, 1875
Subfamily Analytoceratinae Spath, 1927

Species *Analytoceras hermanni* (Gümbel, 1861)

1861. *Ammonites Hermanni* C.W. Gümbel, p. 474; (figured in: Wähner 1894; pl. 3, fig. 3a–b).
1894. *Lytoceras articulatum* (J. Sowerby, 1831) Type B: Wähner; pl. 3, fig. 3a–b.
non 1894. *Lytoceras articulatum* (J. Sowerby, 1831) Type A: Wähner; pl. 7, fig. 1–5; pl. 8, fig. 2–15.
1927. *Monophyllites* (*Trachyphyllites*) *costatus* G. Arthaber, p. 141, pl. 17, fig. 3.
1934. *Trachyphyllites costatus* Arthaber; L.F. Spath, p. 326, text-fig. 112.
1952. *Trachyphyllites costatus* Arthaber; E. Basse, pp. 597–598, 602, fig. 46.3a–b.
1957. *Trachyphyllites costatus* Arth.; W.J. Arkell *et al*., p. L187, fig. 217, 1a,b.
1958. *Trachyphyllites costatus* Arth.; V.V. Drushchits In: V.V. Luppov, p. 70.
1961. *Trachyphyllites costatus*Arth.; O.H. Schindewolf, p. 85, text-fig. 42.
1966a. Trachyphyllites Arthaber; J. Wiedmann, p. 56.
1967. *Trachyphyllites costatus* Arth.; C. Teichert, p. 194.
1968. Trachyphyllites Arthaber; O.H. Schindewolf, p. 56 (748).
1970. *Trachyphyllites costatus* Arthaber; J. Wiedmann, p. 939 ff., text-fig. 8a–b, pl. 5, fig. 6.
1970. *Trachyphyllites costatus* Arthaber; J. Wiedmann and J. Kullmann, text-fig. 14 f.
1971a. *Trachyphyllites costatus* Arthaber; E.T. Tozer, p. 565.
1971b. *Trachyphyllites*; E.T. Tozer, p. 1003.
1973. *Trachyphyllites*; J. Wiedmann, p. 171, 172, 175.
1974. *Trachyphyllites*; V.V. Drushchits and I.A. Mikhailova, p. 470.
1975. *Trachyphyllites*; J. Guex, p. 203, 205.
1976. *Trachyphyllites costatus*; U. Lehmann, p. 44, 45, text-fig. 38, 157
1978. *Trachyphyllites*; L. Krystyn, p. 67.
1981. *Trachyphyllites*; E.T. Tozer, p. 84.

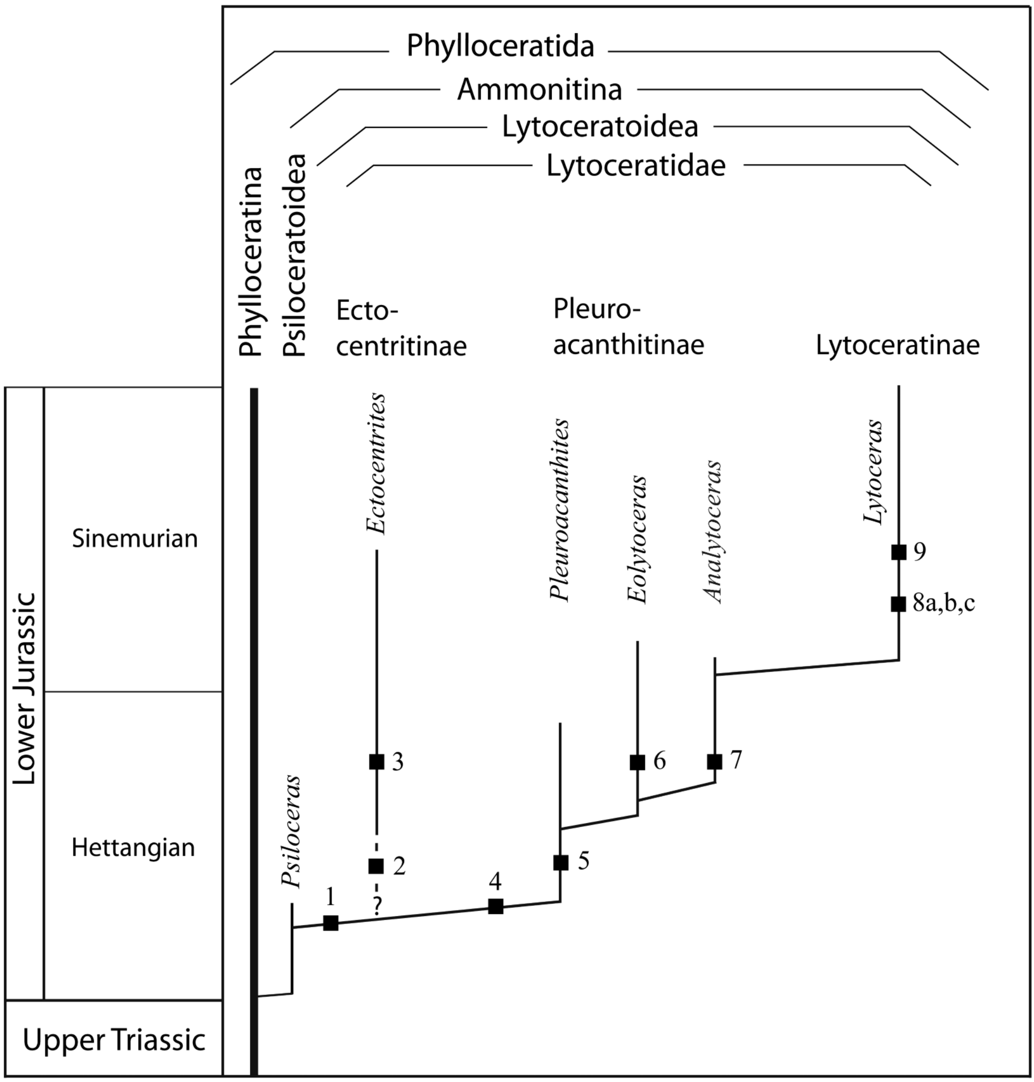


Text-fig. 5. Relationship of Uw/D and WER clearly separates *Analytoceras hermanni* (Gümbel) including "*Trachyphyllites costatum* Arthaber" (▲) from *Analytoceras articulatum* (J. Sowerby) (♦) by their different morphospace

1981. *Trachyphyllites*; J. Wiedmann and J. Kullmann, p. 238, text-fig. 13f.
1982. *Trachyphyllites*; L. Krystyn, p. 57.
1986. *Trachyphyllites*; C. Teichert, p. 235.
1988. *Trachyphyllites*; C. Teichert, p. 60.
1999. *Trachyphyllites*; L. Krystyn, p. 66.
2002. *Trachyphyllites costatus*; A. Sprey, p. 92.
2008. *Analytoceras* sp.; R. Hoffmann and H. Keupp, p. 246, fig. 10 (left-hand side)
2009. *Analytoceras* cf. *articulatum* (Sow.); H. Keupp; fig. 6.

CONCLUSIONS

Due to the morphological consistency of the Bihati specimens (including Arthaber's specimen of "*Trachyphyllites costatus*"), which is clearly distinguished from morphotypes of *Analytoceras articulatum*, "Type A" (see Text-fig. 5), we re-establish the species name *Analytoceras hermanni* (Gümbel, 1861) for Wähner's "Type B" form of *Analytoceras articulatum*, including "*Trachyphyllites costatus* Arthaber, 1927" as a junior subjective synonym.



Text-fig. 6. Phylogeny of lower Jurassic lytoceratid ammonoids with *Analytoceras* as direct ancestor of *Lytoceras* modified after Hoffmann (2009); black boxes represent apomorphic characters: 1 – tendency to generate a septal lobe (intermediate) attached to the basis of the preceding septum (Lytoceratoidea). 2 – strong ornamented, simple, straight ribs with nodes and spines (Ectocentritinae). 3 – ventrolateral nodes or spines, juveniles with regular constrictions becoming weak to nearly unrecognisable to the naked eye in the adult stage (*Ectocentrites*). 4 – parabolic ribs (Pleuroacanthitinae). 5 – feeble ventral median keel (*Pleuroacanthites*). 6 – weak ventrolateral parabolic nodes (*Eolytoceras*). 7 – fimbriate growth lines, high-crested parabolic ribs with ventrolateral nodes and spines (*Analytoceras*). 8a – septal lobe attached to the surface of the preceding septum. 8b – fimbriate ribs with parabolic ribs transformed to flares. 8c – bifid L lobe at the adult stage (Lytoceratinae). 9 – fimbriate flares (*Lytoceras*)

Acknowledgements

We are grateful for financial support for DFG Project Ke 322/32-1 and to Jan Evers for taking the photographs of our specimens. The field excursion to Timor in 2008 was successful only through financial support by the Freie Universität Berlin, the care of our home team of Timor, particularly through the support of the King of Amarassi Province, Robert Koroh, our logistic guide, Junis Tacoy, our field guide, Simon Koroh, and last but not least the engaged helps by Mr. B. Sumbajak, from the Indonesian Embassy in Berlin. Many thanks to all! The authors are indebted to Reinhart Veit, Velden, for the loan of one of the three described specimens of *A. hermanni*. J. Guex, C.J. Wood and an anonymous reviewer improved the manuscript through careful reviews.

REFERENCES

Arkell, W.J. 1950. A classification of the Jurassic ammonites. *Journal of Paleontology*, **24**, 354–364.

Arkell, W.J., Furnish, W.M., Kummel, B., Miller, A.K., Moore, R.C., Schindewolf, O.H., Sylvester-Bradley, P.C. and Wright, C.W. 1957. Mesozoic Ammonoidea. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology Part L Mollusca 4 Cephalopoda Ammonoidea, pp. 1–490. University of Kansas Press & Geological Society of America; Lawrence.

Arthaber, G.v. 1927. Ammonoidea Leiostraca aus der Oberen Trias von Timor. Jaarboek van het Mijnwezen in Nederlandsch Oost-Indië, Verhandelingen, 1926.II, 1–174.

Basse, E. 1952. Ammonoidea s. str. In: J. Pivetaut (Ed.), Traité de Paleontologie Tome 2, pp. 581–688. Paris; Masson.

Basse, E. 1968. Mise en évidence du Carnien dans la zone de Golija (Serbie Centrale, Yougoslavie). *Comptes Rendus Académie des Sciences, Paris, Série D*, **267**, 1270–1272.

Bertinelli, A., Nannarone, C., Passeri, L. and Venturi, F. 2004. Hettangian ammonites and radiolarians in the Mt. Camicia (Gran Sasso, Central Apennines). *Rivista Italiana di Paleontologia e Stratigrafia*, **110**, 87–95.

Besnossov, N.V. and Mikhailova, I.A. 1985. Higher taxa of Jurassic and Cretaceous Lytoceratida. *Biuletyn Moskovskovo Obschestva Ispytatelei Pripody. Otdel Geologia*, **60**, 100–113. [In Russian]

Canavari, M. 1882. Beiträge zur Fauna des unteren Lias von Spezia. *Palaeontographica*, **29**, 123–192.

Canavari, M. 1888. Contribuziona alla Fauna del Lias inferiore Di Spezia. *Memorie del Regio Comitato Geologico d´Italia*, **3**, 57–227.

Dommergues, J.-L. 1994. Les faunes d´ammonites pandémiques et téthysiennes du Lias confrontées à un modèle de distribution pantropicale. *Palaeopelagos Special Publication*, **1**, 93–107.

Drushchits, V.V. 1958. Superfamily Lytocerataceae. In: N.P. Luppov and V.V. Drushchits (Eds), Fundamentals of palaeontology: Mollusca – Cephalopoda II. Ammonoidea (Ceratitida and Ammonitida), Endocochlia, pp. 56–61. Gosudarstvennoe Naucho-tehniceskoe Izdatel'stv; Moskva. [In Russian]

Drushchits, V.V. 1976. Superfamily Lytocerataceae. In: N.P. Luppov and V.V. Drushchits (Eds), Fundamentals of Paleontology: 6. Mollusca – Cephalopoda II. Israel Program for Scientific Translations; Jerusalem. [English translation of Drushchits, V.V. 1958]

Drushchits, V.V. and Mikhailova, I.A. 1974. On the systematics of early Cretaceous ammonites. *Paleontological Journal*, **8**, 37–48.

Drushchits, V.V., Bogoslovskaya, M.F. and Doguzhayeva, L.A. 1976. Evolution of septal necks in the Ammonoidea. *Paleontological Journal*, **10**, 37–50.

Fucini, A. 1923. Fossili domeriani dei Dintorni di Taormina 3. *Palaeontographia Italica*, **29–30**, 41–77.

Guex, J. 1987. Sur la phylogenése des ammonites du Lias inferieur – Phylogeny of lower liassic ammonites. *Bulletin de la Societe Vaudoise des Sciences Naturelles*, **78**, 455–469.

Guex, J. 1995. Ammonites hettangiennes de la Gabbs Valley Range (Nevada). *Mémoires de Géologie, Lausanne*, **27**, 1–131.

Guex, J. and Taylor, D. 1976. La limite Hettangien-Sinémurien, des Préalpes romandes au Nevada. *Eclogae Geologicae Helveticae*, **69**, 521–526.

Guex, J., Bartolini, A., Atudorei, V. and Taylor, D. 2004. High-resolution ammonite and carbon isotope stratigraphy across the Triassic Jurassic boundary at New York Canyon (Nevada). *Earth and Planetary Science Letters*, **225**, 29–41.

Gümbel, C.W. 1861. Geognostische Beschreibung des bayerischen Alpengebirges und seines Vorlandes, pp. 1–950. Perthes; Gotha.

Hillebrandt, A.v. 2000. Die Ammoniten-Fauna des südamerikanischen Hettangium (basaler Jura). Teil 3. *Palaeontographica, Abteilung A*, **258**, 65–116.

Hoffmann, R. 2009. New Insight on the Phylogeny of the Lytoceratoidea (Ammonitina) from the septal lobe and its functional interpretation. 242 pp. Freie Universität Berlin. Unpublished PhD.

Hoffmann, R. and Keupp, H. 2008. Ammoniten, die man kennen muss: Lytoceraten. *Fossilien*, **4**/2008, 242–249.

Houša, V. 1965. Sexual dimorphisms and the system of Jurassic Cretaceous Ammonoidea. *Casopis Narodního Muzea*, **134**, 33–35.

Hölder, H. 1975. Forschungsbericht über Ammoniten. *Paläontologische Zeitschrift*, **49**, 493–511.

Hyatt, A. 1889. Genesis of the Arietidae. *Smithsonian Contributions to Knowledge*, **16**, 1– 238.

Hyatt, A. 1900. Cephalopoda. In: C.R. Eastman (Ed.), Textbook of Paleontology, 1st English Edition. pp. 502–604. London. [adapted from the German of Karl A. von Zittel]

Kennedy, W.J. 1977. Ammonite Evolution. In: A. Hallam (Ed.), Patterns of Evolution, pp. 251–304. Elsevier; Amsterdam – Oxford – New York.

Kennedy, W.J. and Klinger, H.C. 1978. Cretaceous faunas from Zululand and Natal, South Africa. The ammonite family Lytoceratidae Neumayr, 1875. *Annals of the South African Museum*, **74**, 257–333.

Keupp, H. 2009. Timor: Bonanza nicht nur für Triasfossilien. *Fossilien*, **4**/2009, 214–220.

Krumbeck, L. 1923. Zur Kenntnis des Juras der Insel Timor. In: J. Wanner (Ed.), Paläontologie von Timor nebst kleineren Beiträgen zur Paläontologie einiger anderer Inseln des Ostindischen Archipels. XII Lieferung, pp. 1–120. Stuttgart.

Krystyn, L. 1978. Eine neue Zonengliederung im alpin-mediterranen Unterkarn. In: H. Zapfe (Ed.), Beiträge zur Biostratigraphie der Tethys-Trias, pp. 37–75.

Krystyn, L. 1982. Obertriassische Ammonoideen aus dem Zentralnepalesischen Himalaya (Gebiet von Jomsom). *Abhandlungen der Geologischen Bundesanstalt, Wien*, **36**, 1–63.

Krystyn, L. 1999. A Major Phylloceratid-Lytoceratid Faunal Turnover in the Lower Jurassic. In: K. Histon (Ed.), Cephalopods – Present and Past – V International Symposium, Abstract Volume. *Berichte der Geologischen Bundesanstalt*, **46,** 66.

Lehmann, U. 1976. Ammoniten – Ihr Leben und ihre Umwelt, pp. 1–171. Enke; Stuttgart.

Lehmann, U. 1990. Ammonoideen. In: H.K. Erben, G. Hillmer and H. Ristedt (Eds), Haeckel-Bücherei 2, pp. 1–257. Enke; Stuttgart.

Lucas, S.G. and Tanner, L.H. 2004. Late Triassic extinction events. *Albertiana*, **31**, 31–40.

Mostler, H. and Scheuring, B. and Urlichs, M. 1978. Zur Mega-, Mikrofauna und Mikroflora der Kössener Schichten (alpine Obertrias) vom Weißloferbach in Tirol unter besonderer Berücksichtigung der in der suessi- und marshi-Zone auftretenden Conodonten. *Österreichische Akademie der Wissenschaften Schriftenreihe der Erdwissenschaftlichen Kommissionen Band*, **4**, 141–174.

Neumayr, M. 1875. Die Ammoniten der Kreide und die Systematik der Ammonitiden. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **27**, 854–892.

Salfeld, H. 1924. Die Bedeutung der Konservativstämme für die Stammesentwicklung der Ammonoideen, pp. 1–16. Max Weg; Leipzig.

Schindewolf, O.H. 1961. Studien zur Stammesgeschichte der Ammoniten; Lieferung 1. *Abhandlungen der Akademie der Wissenschaften und der Literatur in Mainz, Mathematisch-Naturwissenschaftliche Klasse*, 1960 (10), 639 (5) – 743 (109).

Schindewolf, O.H. 1968. Studien zur Stammesgeschichte der Ammoniten; Lieferung 7. *Abhandlungen der Akademie der Wissenschaften und der Literatur in Mainz, Mathematisch-Naturwissenschaftliche Klasse*, 1968 (3), 41 (733) – 209 (901).

Shevyrev, A.A. 1968. Triassic ammonoids from the south of SSSR. *Trudy Paleontologičeckogo Instituta*, **119**, 1–272. [In Russian]

Shigeta, Y. 2006. Ammonoid evolution inferred for the early shell features. *Iden*, **60**, 23–26.

Sowerby, J. 1831. Section VI. Oolitic Group. In: H.T. De La Beche (Ed.), A Geological Manual, pp. 314–352. London.

Spath, L.F. 1927. Revision of the Jurassic cephalopod fauna of Kachh (Cutch) – Part 1. *Memoirs of the Geological Survey of India*, **9**, 1–71.

Spath, L.F. 1934. Catalogue of the Fossil Cephalopoda in the British Museum (Part 4, 5), The Ammonoidea of the Trias, pp. 1–521. London.

Sprey, A.M. 2002. Morphometrie und Paläoökologie von Ammonoideen vor, während und nach globalen Faunenkrisen. *Münstersche Forschungen zur Geologie und Paläontologie*, **95**, 1–158.

Suess, E. 1865. Über Ammoniten. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften*, **52**, 3–19.

Teichert, C. 1967. Major Features of Cephalopod Evolution. Essays in Paleontology and Stratigraphy, Special Publication, 2, 162–210.

Teichert, C. 1986. Times of crisis in the evolution of the Cephalopoda. *Paläontologische Zeitschrift*, **60**, 227–243.

Teichert, C. 1988. Main Features of Cephalopod Evolution. In: M.R. Clarke, E.R. Trueman (Eds), and K.M. Wilbur (Chief Ed.), The Mollusca. Marine Biological Association of the United Kingdom, 12, 11–79.

Tozer, E.T. 1971a. One two or three connecting links between Triassic and Jurassic ammonoids? *Nature*, **232**, 565–566.

Tozer, E.T. 1971b. Triassic time and ammonoids: problems and proposals. *Canadian Journal of Earth Science*, **8**, 989–1031.

Tozer, E.T. 1981. Triassic Ammonoidea: Classification, Evolution and Relationship with Permian and Jurassic Forms. In: M.R. House and J.R. Senior (Eds), The Ammonoidea. The Systematics Association Special Volume, 18, 65–100.

Venturi, F. and Bilotta, M. 2008. New data and hypotheses on early Jurassic ammonite phylogeny. *Revue de Paléobiologie*, **27**, 859–901.

Wähner, F. 1894. Beiträge zur Kenntnis der tieferen Zonen des unteren Lias in den nordöstlichen Alpen – Teil 7. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients*, **9**, 1–54.

Welter, O. 1914. Die obertriadischen Ammoniten und Nautiliden von Timor. In: J. Wanner (Ed.), Paläontologie von Timor nebst kleineren Beiträgen zur Paläontologie einiger anderer Inseln des Ostindischen Archipels. I Lieferung, pp. 1-258. Stuttgart.

Wendt, J. 1970. Stratigraphische Kondensation in triadischen und jurassischen Cephalopodenkalken der Tethys. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1970 (7)**, 433–448.

Wiedenmayer, F. 1978. Exomiloceras (Analytoceratidae, Ammonoidea), eine neue Gattung aus dem unteren Lias der Tethys. *Eclogae Geologicae Helvetiae*, **72**, 859–870.

Wiedmann, J. 1964. Unterkreide-Ammoniten von Mallorca 2. Lieferung: Phylloceratina. *Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse Jahrgang*, **1963 4**, 151–256.

Wiedmann, J. 1966a. Stammesgeschichte und System der posttriadischen Ammonoideen – Ein Überblick (1. Teil). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **125**, 49–79.

Wiedmann, J. 1966b. Stammesgeschichte und System der posttriadischen Ammonoideen – Ein Überblick (2. Teil). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **127**, 13–81.

Wiedmann, J. 1970. Über den Ursprung der Neoammonoideen – Das Problem der Typogenese. *Eclogae Geologicae Helvetiae*, **63**, 923–1020.

Wiedmann, J. 1972. Ammoniten-Nuklei aus Schlämmproben der nordalpinen Obertrias – ihre stammesgeschichtliche und stratigraphische Bedeutung. *Mitteilungen der Gesellschaft der Geologie- und Bergbaustudenten*, **21**, 561–622.

Wiedmann, J. 1973. Evolution or revolution of ammonoids at Mesozoic system boundaries. *Biological Reviews*, **48**, 159–194.

Wiedmann, J. and Kullmann, J. 1981. Ammonoid sutures in Ontogeny and Phylogeny. In: M.R. House and J.R. Senior (Eds), The Ammonoidea. The Systematics Associatio Special Volume, 18, 215–255.

Zittel, K.A. 1884. Handbuch der Palaeontologie. I Abtheilung Palaeozoologie II. Band. Mollusca und Arthropoda, pp. 1–893. R. Oldenbourg; München und Leipzig.

Manuscript submitted: 20th July 2009
Revised version accepted: 15th May 2010